# VOLATILE EMISSIONS TRIGGERED BY MULTIPLE HERBIVORE DAMAGE: BEET ARMYWORM AND WHITEFLY FEEDING ON COTTON PLANTS

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**Abstract**—Plants are commonly attacked by more than one species of herbivore, potentially causing the induction of multiple, and possibly competing, plant defense systems. In the present paper, we determined the interaction between feeding by the phloem feeder silverleaf whitefly (SWF), *Bemisia tabaci* Gennadius (B-biotype = *B. argentifolii* Bellows and Perring), and the leaf-chewing beet armyworm (BAW), *Spodoptera exigua* Hübner, with regard to the induction of volatile compounds from cotton plants. Compared to undamaged control plants, infestation with SWF did not induce volatile emissions or affect the number and density of pigment glands that store volatile and nonvolatile terpenoid compounds, whereas infestation by BAW strongly induced plant volatile emission. When challenged by the two insect herbivores simultaneously, volatile emission was significantly less than for plants infested with only BAW. Our results suggest that tritrophic level interactions between cotton, BAW, and natural enemies of BAW, that are known to be mediated by plant volatile emissions, may be perturbed by simultaneous infestation by SWF. Possible mechanisms by which the presence of whiteflies may attenuate volatile emissions from caterpillar-damaged cotton plants are discussed.

**Key Words**—*Bemisia argentifolii*, silverleaf whitefly, *Spodoptera exigua*, beet armyworm, *Gossypium hirsutum*, cotton, herbivore-induced volatiles.

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INTRODUCTION

Studies on induced plant defenses have mostly addressed the effects of damage by a single species of herbivore (Karban and Baldwin, 1997). These studies have shown that herbivore infestation of plants typically induces metabolic pathways that lead to altered levels of certain allelochemicals (Karban and Baldwin, 1997) or emission of volatile compounds that attract natural enemies of the herbivores (Dicke and Vet, 1999). These plant responses differ based on the type of feeding damage inflicted by the species of herbivores (Walling, 2000). Leaf-chewing insects typically induce the jasmonic acid (JA) pathway in plants, whereas phloem-feeding insects induce the salicylic acid (SA) pathway (Walling, 2000; Bostock et al., 2001). This specificity in a plant's response to herbivore damage is particularly important because plants throughout their life cycle are often exposed to simultaneous damage by multiple species of herbivores (e.g., Thompson, 1998).

Induction of a specific plant metabolic system by a particular herbivore may be altered if the plant is simultaneously challenged with one or more additional species of herbivores. For instance, induction of the SA defense pathway may inhibit the JA pathway, and vice versa (e.g., Fidantsef et al., 1999; Thaler et al., 2002). Consequently, we might expect that plant defense response to infestation by a specific herbivore would be perturbed upon simultaneous infestation by additional herbivores, particularly if they belong to different feeding guilds. Stout et al. (1998), for example, found that aphids (phloem feeders) caused tomato plants to become more susceptible to caterpillar damage.

Perturbations in plant defense responses when challenged by more than one herbivore species may impact tritrophic level interactions, i.e., interactions between plants and the natural enemies of herbivores. In particular, damage by more than one species of herbivore may alter emission of plant volatiles that attract natural enemies of the herbivores (Shiojiri et al., 2001; Vos et al., 2001). Shiojiri et al. (2001) found that cabbage plants damaged by two species of Lepidoptera emit a different blend of volatiles compared to those infested by a single species, e.g., the amount of ($E$)-4,8-dimethyl-1,3,7-nonatriene from plants infested by both herbivores was not as high as that from plants infested by a single species. Yet, we are not aware of any studies that have investigated the effects of combined damage by two species of insects with different feeding habits on the emission of volatiles in plants.

In cotton, feeding by leaf-chewing caterpillars and piercing-sucking hemipter-ans induces the production of volatiles (McCall et al., 1994; Rodriguez-Saona et al., 2002). Herbivore damage may induce volatile emissions in cotton by activation of the JA-pathway (Rodriguez-Saona et al., 2001). Also, herbivore feeding may increase volatile emissions in plants by inducing changes in the number, density, or chemistry of pigment glands (McAuslane et al., 1997; Agrawal and Karban, 2000), where large amounts of constitutive terpenoid volatiles are stored

(Elzen et al., 1985). For instance, damage to pigment glands by caterpillar feeding causes the release of high quantities of these stored compounds (Paré and Tumlinson, 1997; McAuslane and Alborn, 2000). However, it remains unknown whether these responses are also induced when cotton plants are damaged by phloem-feeding (Homoptera) insects.

This study investigates volatile emissions in cotton following feeding by the phloem feeder silverleaf whitefly (SWF), *Bemisia tabaci* Gennadius (B-biotype = *B. argentifolii* Bellows and Perring) (Homoptera: Aleyrodidae), when feeding alone or in combination with the leaf-chewing caterpillar beet armyworm (BAW), *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae). Both insects are common pests on cotton and share similar habitats across the United States. We addressed the following specific objectives: First, we determined if SWF infestation induces volatile emissions or affects the number and density of pigment glands in cotton plants. Second, we investigated whether SWF infestation affects induction of volatiles by BAW damage and if so, if BAW leaf consumption was altered when feeding on SWF-damaged plants.

## METHODS AND MATERIALS

*Plants and Insects.* Glanded cotton, *Gossypium hirsutum* L. cv. Delta Pine 5415, was grown as described in Rodriguez-Saona et al. (2001) and used for all experiments. Plants were grown in greenhouses under natural light supplemented with 2000 $\mu$mol/m$^2$/sec max daily photosynthetically active radiation and fertilized three times a week with 750 ml of a 2-g/l solution of 20-20-20 N-P-K fertilizer (Grow More, Gardena, California). A whitefly, *B. tabaci* B-biotype, colony was maintained on cotton plants in greenhouse cages (90 × 90 × 90 cm) at 30°C and 30% RH. *Spodoptera exigua* larvae were reared on an alfalfa-based diet as described by Rodriguez-Saona et al. (2001). Both colonies were maintained at the Western Cotton Research Laboratory, Phoenix, AZ.

*Volatile Collections.* Volatiles were collected in greenhouses as described by Rodriguez-Saona et al. (2001). The collection apparatus consisted of a push/pull system (Heath and Manukian, 1994) where charcoal purified air enters the top of a 42.5 cm high and 18 cm diam glass chamber over a plant at a rate of 5 l/min. Volatiles were collected on Super-Q adsorbent (Alltech, Deerfield, IL) filter traps by pulling air from the chambers at 1 l/min. The remaining air was vented from the chambers through an opening around the stem of the plant loosely sealed with cotton. Four independent chambers allowed for simultaneous collections of volatiles from four different cotton plants.

Volatile samples were analyzed as described in Rodriguez-Saona et al. (2001). Cotton volatiles were eluted from traps with 180 $\mu$l of methylene chloride. An internal standard (600 ng of *n*-octane in 5 $\mu$l of methylene chloride) was added to the extract. One-microliter aliquots were injected into an Hewlett-Packard gas

chromatograph (GC model 6890) equipped with a capillary injector system, a flame ionization detector, an auto injector model 7683, and an HP1 methyl siloxane column (30 m × 0.32 mm ID, 0.25-$\mu$m film). The GC was programmed in a split mode (25:1), and helium was used as a carrier gas at a linear flow velocity of 40 cm/sec. Following injection, oven temperature was maintained at 50°C for 3 min, programmed to rise to 190°C at 5°C/min, and then maintained at this temperature for 5 min. Data were analyzed with Hewlett-Packard ChemStation software.

For each sample, amounts of the detected volatiles were based on comparison of their peak areas with that of the internal standard. Individual compounds were identified by comparing their retention times with those of commercially available standards and by comparing their mass spectra standards to those available in a database from the National Institute of Standards and Technology.

*Volatiles from Whitefly-Infested Plants.* Cotton seedlings (2-wk old) with two cotyledons and two expanded leaves were exposed for 48 hr to *B. tabaci* adults (approx. 500–600) for oviposition. This density ensured high levels of infestation without killing the plant. Insects were caged with plants in 26 cm diam and 60 cm high Plexiglass cylinder chambers with the top of each chamber covered by a fine nylon mesh to allow air circulation. The chamber also had a 14-cm diam opening in the middle covered with nylon that allowed for manipulation of plants and insects inside the chambers. After oviposition, all SWF adults were removed from plants with the use of an aspirator, and plants were allowed to grow for 3–4 wk before volatiles were collected, such that the majority of nymphs (>80%) had reached the 3rd or 4th stadium. We collected volatiles from cotton infested with SWF nymphs or nymphs and adults because plants can respond differently to feeding by these two stages (van de Ven et al., 2000). In cases where volatiles were collected from plants infested by adults and nymphs, *B. tabaci* adults were reintroduced into the chambers 4 d prior to volatile collections and removed as described above on the day volatiles were collected. Control plants were subjected to the same conditions (caged), but had no whiteflies. Volatiles from SWF-infested cotton plants, which included the plant, whitefly nymphs, and nymphal secretions, and from SWF-free plants were collected in a greenhouse concurrently for two consecutive days during the times of maximal emissions (1000–1800 hr; Rodriguez-Saona et al., 2001). Each plant was considered a replicate, and treatments were replicated 3–4 times.

It is possible that whitefly infestation might affect volatile emissions in plants because of changes in number or density of cotton glands, where large amounts of terpene volatiles are stored (Elzen et al., 1985). Thus, we compared the number and density of glands on whitefly-infested and noninfested plants. After volatiles were collected, all leaves from each SWF-infested and SWF-free plant were excised, bagged, and labeled. Leaf area from each leaf was measured using a leaf area meter (LI-3100, LI-COR Inc., Lincoln, NE). In addition, total number of nymphs and pigment glands from a 3.88$-$ and 1.0$-$cm$^2$ leaf disk, respectively, were recorded

from each leaf. Leaf disks were taken from an area located at the center of the leaf, left of the central vein, and on the abaxial surface (Naranjo and Flint, 1994; Chu et al., 2000). Both SWF nymphs and pigment glands were counted with the aid of a microscope. To aid in pigment gland counting, leaf disk surfaces were gently scrapped.

*Interactions between Insects.* Amounts of *S. exigua*-induced cotton volatiles when feeding on SWF-free and SWF (nymphs)-infested plants were investigated. Cotton plants were exposed to *B. tabaci* as described above, such that plants were infested with nymphs for 3–4 wk before they were presented to BAW for feeding. After treatment, plants were placed in volatile collection chambers at 1000 hr with 10 3rd instar BAW. Larvae were allowed to feed on plants for 24 hr, while volatile emissions were collected continuously during the same time period. Total leaf area removed by caterpillar feeding was obtained by scanning leaves and measuring area consumed using RE-650N computer software (Canon, Lake Success, NY). Each treatment was replicated 4–5 times.

*Statistical Analysis.* Differences in total volatile production and consumption among treatments were analyzed using a completely randomized analysis of variance (ANOVA; Systat ver. 9, 1998; SPSS Science, Chicago, IL). Differences in volatile emissions among undamaged control plants, plants infested with SWF nymphs and adults, and those infested only by nymphs were compared using ANOVA. Similarly, we used ANOVA to compare volatile emissions between plants damaged only by caterpillars to those from plants damaged by caterpillars and nymphs. Each plant was treated as a replicate in the analyses. In cases where significant differences were detected among treatments, a multiple comparison Tukey test was used. A nested ANOVA design was used to analyze the number and density of glands from SWF exposed or unexposed plants (PROC MIXED; SAS, 1999; SAS Institute, Cary, NC). Differences among treatments were assessed using multiple *t*-tests and adjusted using the Tukey method. Two factors were tested: treatment (uninfested controls, nymph and adult SWF-infested plants, and nymph SWF-infested plants) and leaf position within a plant (from top to bottom: pos1 = leaves on nodes 1 and 2; pos2 = leaves on nodes 3 and 4; pos3 = leaves on nodes 5 and 6; pos4 = leaves on nodes 7 and 8; pos5 = leaves on nodes 9 and 10). Trials were treated as a random variable in the model. The effects of insect density on plant volatiles and gland production were tested using linear regressions. Data were log transformed (natural logarithm) when necessary to correct for heterogeneity of variances.

RESULTS AND DISCUSSION

*Volatiles from Whitefly-Infested Plants.* There is little evidence pertaining to the relationship between insect feeding habit and the induction of plant volatile

emissions. To our knowledge this is the first report that addresses the impact of the phloem-feeding SWF on induction of volatiles in cotton. Under the experimental system we employed, SWF infestation did not lead to induction of plant volatile compounds relative to nondamaged control plants (Figure 1). It is well-documented that leaf-chewing caterpillars induce the synthesis and subsequent emission of terpenoid compounds in cotton (Figure 1; McCall et al., 1994; Paré
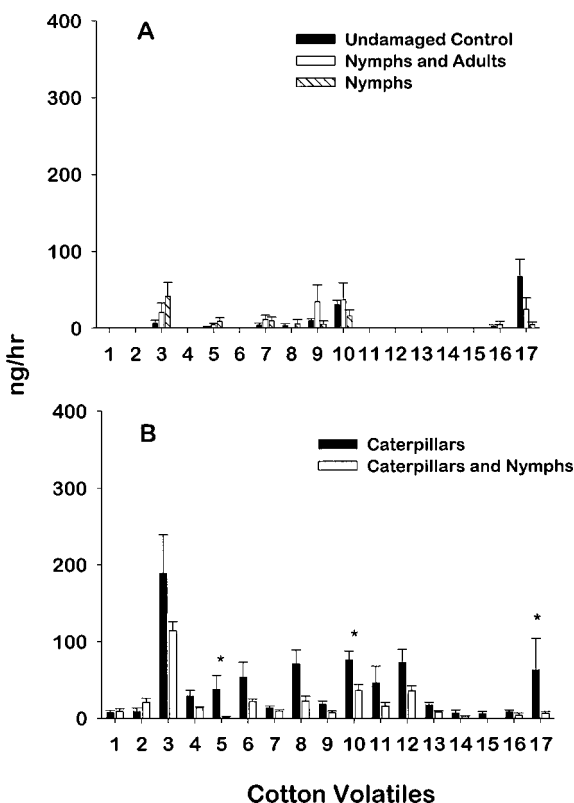


FIG. 1. Volatiles collected from noninfested cotton plants (control) and plants infested with *Bemisia tabaci* B-Biotype nymphs or nymphs and adults (A) and from plants damaged by *Spodoptera exigua* larvae with and without *B. tabaci* nymphs (B): **1** = (*E*)-2-Hexanal; **2** = (*Z*)-3-Hexen-1-ol; **3** = $\alpha$-Pinene; **4** = $\beta$-Pinene; **5** = Myrcene; **6** = (*Z*)-3-Hexenyl acetate; **7** = Limonene; **8** = (*E*)-$\beta$-Ocimene; **9** = Linalool; **10** = (*E*)-4, 8-Dimethyl-1, 3, 7-Nonatriene; **11** = Indole; **12** = (*E*)-$\beta$-Caryophyllene; **13** = $\alpha$-Humulene; **14** = (*E*)-$\beta$-Farnesene; **15** = (*E*, *E*)-$\alpha$-Farnesene; **16** = Nerolidol; **17** = (*E*)-4, 8, 12-Trimethyl-1, 3, 7, 11-Tridecatetraene. Bars represent the mean + 1 SE ($N \geq 3$). An asterisk denotes significant differences among treatments (ANOVA, $P \leq 0.05$).

and Tumlinson, 1997). In contrast, cotton plants infested by SWF nymphs, or adults and nymphs, emitted only slight amounts of the inducible volatiles $(E)$-$\beta$-ocimene, linalool, $(E)$-4, 8-dimethyl-1, 3, 7-nonatriene, and $(E, E)$-4, 8, 12-trimethyl-1, 3, 7, 11-tridecatetraene at levels that were not different from undamaged control plants (ANOVA; $P > 0.05$; Figure 1). Likewise, the total volatile amounts emitted from SWF-infested plants did not differ from controls ($F = 0.42$; $df = 2, 8$; $P = 0.67$; Total volatile emissions: control = $116.8 \pm 25.6$ [ng/hr $\pm$ SE]; nymphs = $135.6 \pm 53.8$; nymphs and adults = $90.0 \pm 36.1$; Figure 1A) and was not affected by varying insect density, i.e., higher levels of SWF infestation did not increase volatile production in cotton (Linear Regression: $F = 2.06$; $df = 1, 4$; $P = 0.23$; $r^2 = 0.34$). Our results are comparable to Turlings et al. (1998) who reported high amounts of volatile emissions from maize attacked by caterpillars, but no measurable emissions of volatiles from plants heavily infested by aphids.

Volatiles emitted from whitefly-infested plants can serve as olfactory cues for parasitoids in host location. For example, *Encarsia formosa* Gahan, a parasitoid of the greenhouse whitefly, *Trialeurodes vaporariorum* Westwood, was more attracted to whitefly-infested bean plants, *Phaseolus vulgaris* L., compared to noninfested plants (Guerrieri, 1997). Birkett et al. (2003) showed that feeding by adults of *T. vaporariorum* elevated the amounts of $(Z)$-3-hexen-1-ol, $(E)$-4, 8-dimethyl-1, 3, 7-nonatriene, and 3-octanone emitted from bean plants compared to noninfested plants. These compounds increased the attractiveness of *E. formosa* towards the odor source (Birkett et al., 2003). Noldus and van Lenteren (1990), however, found a lack of discrimination by *E. formosa* between odors from whitefly-infested and noninfested tomato and cucumber plants. In cotton, cues other than odors emitted from SWF-infested plants, such as visual and contact chemical cues, might play a more important role in host-searching behavior of their parasitoids (e.g., van Lenteren et al., 1976; Shimron et al., 1992; Guerrieri, 1997; Sütterlin and van Lenteren, 2000).

Because insect herbivory may induce production and/or filling of pigment glands that store constitutive volatiles in plants (e.g., McAuslane et al., 1997; Agrawal and Karban, 2000), we tested whether SWF infestation induces changes in the number and density of pigment glands in cotton. In general, pigment glands decreased in density ($F = 29.9$; $P < 0.01$; Figure 2A) and number ($F = 35.3$; $P < 0.01$; Figure 2B) with leaf age. The number of SWF nymphs per cm$^2$ ranged from 0 on top leaves to 150 on leaves from position 4 of infested plants (Figure 2D).

Significant differences among treatments were marginal and only found for gland density at leaf positions 2 and 3 (nested ANOVA; Position within treatment: $F = 29.93$; $df = 12, 73$; $P < 0.01$; $t$-test for position 2: $t = 2.3$; $df = 73$; $P = 0.02$; $t$-test for position 3: $t = 2.85$; $df = 73$; $P < 0.01$; Figure 2A). The nymph density at leaf positions 2 and 3 was small (Figure 2D), and it is likely that the increased gland density at these leaf positions was due to smaller leaf area
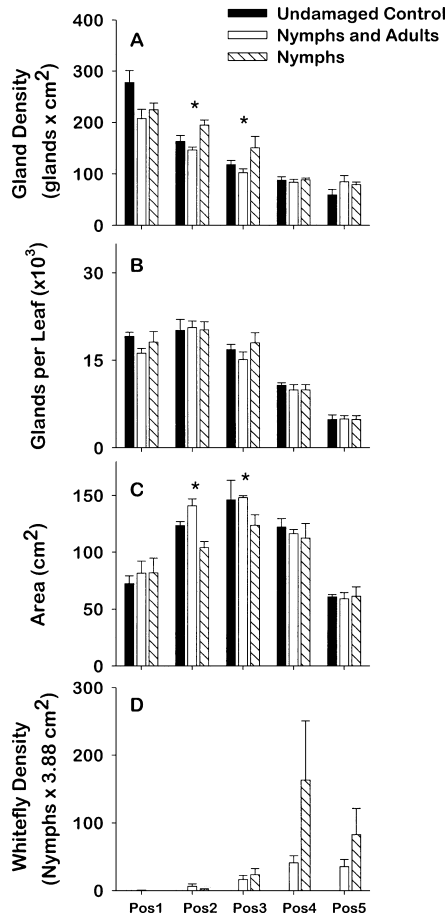
FIG. 2. Gland density (A), leaf area (B), glands per leaf (C), and whitefly density (D) on healthy cotton plants and plants infested with *Bemisia tabaci* B-biotype nymphs or nymphs and adults. Bars represent the mean + 1 SE ($N \geq 3$). The $x$-axis indicates the position of leaves in the plant (from top to bottom): pos1 = leaves on nodes 1 and 2; pos2 = leaves on nodes 3 and 4; pos3 = leaves on nodes 5 and 6; pos4 = leaves on nodes 7 and 8; pos5 = leaves on nodes 9 and 10. An asterisk denotes significant differences among treatments within leaf position (nested ANOVA, $P \leq 0.05$).

(nested ANOVA; Position within treatment: $F = 17.63$; $df = 12, 73$; $P < 0.01$; $t$-test for position 2: $t = 3.34$; $df = 73$; $P < 0.01$; $t$-test for position 3: $t = 2.2$; $df = 73$; $P = 0.03$; Figure 2C). There was no effect of SWF infestation on gland number at any leaf position (Figure 2B). Overall, our results indicate that there is little to no effect of SWF infestation on leaf gland number or density.

*Interactions between Insects.* Given that feeding by multiple species of herbivores can influence emissions of volatiles in plants (Shiojiri et al., 2001; Vos et al., 2001), we investigated how SWF infestation affected the production of volatiles induced by BAW in cotton. Although the blend of compounds emitted from plants infested with SWF nymphs plus BAW was qualitatively similar to those damaged by BAW alone, we found a 60% reduction in the magnitude of volatile emissions from plants attacked by SWF plus BAW as compared to those damaged only by BAW ($F = 9.17; df = 1, 7; P = 0.02$; Total volatile emissions: BAW $= 713.4 \pm 131.6$ [ng/hr $\pm$ SE]; BAW plus SWF $= 311.3 \pm 27.1$; Figure 1B). Such a reduction in volatile emissions may have important consequences for the attraction of natural enemies of herbivores. For example, Fritzsche et al. (2002) tested the attractiveness of the parasitoid *Cotesia marginiventris* (Cresson) to varieties of maize that differ in the quality and quantity of emitted volatiles. They reported that cultivars that emitted lower amounts of volatiles upon herbivory were less attractive to parasitic wasps. In our experiments, the majority of individual compounds from the cotton blend were emitted in lower amounts from BAW- plus SWF-infested plants as compared to plants damaged by BAW alone (Figure 1B). In particular, three compounds, myrcene, (*E*)-4, 8-dimethyl-1, 3, 7-nonatriene, and (*E*, *E*)-4, 8, 12-trimethyl-1, 3, 7, 11-tridecatetraene, were emitted in significantly lower amounts ($P < 0.05$; Figure 1B).

At least three nonmutually exclusive mechanisms may operate to reduce caterpillar-induced volatiles from SWF-infested plants. First, SWF feeding may affect the number or density of pigment glands that store constitutive volatiles, or the amounts of volatile chemicals stored in glands. We found little support for an effect of SWF feeding on the number or density of glands in cotton leaves (Figure 2), however, changes in gland chemistry were not investigated.

Second, because amounts of leaf area consumption by caterpillar damage is positively correlated with plant volatile emissions (e.g., Gouinguené et al., 2003), we hypothesized that decreased leaf consumption by BAW in the presence of SWF may be a factor associated with the observed decrease in volatile emissions. For instance, Inbar et al. (1999) reported reduced growth and development of young, but not older, instars of *Trichoplusia ni* (Hübner) on SWF-infested collard plants. Although larval consumption was not measured, they indicated that whitefly-infested plants could reduce the caterpillar's growth through direct physical interference and/or by the elevated foliar levels of chitinases, ß-1, 3-glucanases, and peroxidases on SWF-infested collard leaves as compared to uninfested controls. We found a trend towards reduced amounts of foliage consumed by caterpillars from SWF-infested plants as compared to uninfested plants, however, the difference between the two treatment means was not statistically significant ($F = 0.702; df = 1, 6; P = 0.434$; Leaf area removed: control $= 219.1 \pm 50.9$ [$cm^2 \pm$ SE]; SWF $= 119.6 \pm 14.1$).

Finally, SWF feeding may induce a response in plants that perturbs the induction of volatile emissions by BAW. Phloem-feeding herbivores, such as the SWF, induce the SA-signaling pathway in plants (Mayer et al., 1996; Walling, 2000). There is evidence that the induction of the SA pathway can negatively impact the induction of the JA pathway (Fidantsef et al., 1999; Thaler et al., 2002). Considering that the JA-signaling pathway is involved in the production of caterpillar-induced volatiles in cotton (Rodriguez-Saona et al., 2001), the decrease in volatile emissions in the presence of SWF could be associated with the induction of the SA pathway by SWF. Further research will be needed to accept or reject fully any of these mechanisms.

In summary, we found that volatiles emitted from plants in response to insect damage can vary with insect feeding habits (also see Turlings et al., 1998). Specificity in plant volatiles induced by different herbivores may have important implications for the types of cues natural enemies use in host location (e.g., De Moraes et al., 1998; Röse et al., 1998). Our data show that SWF feeding did not induce volatile production in cotton plants. However, we found evidence that SWF infestation did reduce amounts of volatile emissions triggered by the leaf-chewing BAW. Recently, Shiojiri et al. (2000) and Vos et al. (2001) showed that the presence of nonhosts on a host-infested plant can interfere with the attraction of parasitoids, weakening interaction strengths between parasitoids and their hosts. In the present study, we have shown that damage by a phloem-feeder such as SWF can potentially interfere in the production of volatiles induced by chewing caterpillars. However, it remains to be determined whether these interguild interactions result in changes in the host searching behavior of natural enemies.

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